

and location of all stages of coral reproductive cycles, including recruitment and growth. Reproductive stages for each species are susceptible to different impacts at particular times of the year, corresponding to spatial and temporal variation of reproductive activities. Because of the open nature of the marine system, the ultimate effect of any localized impact is also likely to be incurred by one or more sink reef areas within the region of the metapopulation, even those remote from the reproductive source area (Keough and Black 1996, Raimondi and Reed 1996).

Negative impacts to one or multiple stages of the reproductive process are likely to have a cascading effect on the success of the remaining stages. For instance, Hughes et al. (2000) discovered a strong link between adult fecundity and recruitment in species of Australian *Acropora* and suggested that even a small decline in fecundity will result in a major reduction in overall recruitment. Small changes in fertilization rates or the rate of mortality of embryos and larvae also may have dramatic effects on the recruitment of dispersing offspring (Underwood and Fairweather 1989, Levitan 1995, Lasker et al. 1996). The onset and rate of coral gamete development appear to be influenced by environmental cues and conditions (Szmant-Froelich et al. 1980, Harrison and Wallace 1990, Szmant and Gassman 1990, Fan and Dai 1999). Physical and/or chemical impacts to the benthic community over the course of gamete maturation thus have the potential to disrupt the development process, resulting in loss of synchronization and/or a reduction in overall fecundity. Sedimentation, reduced salinity from runoff, oil residues and dispersants, heavy metals, and various chemical waste products may interfere with fertilization, embryonic development, and coral planula survival (Acevedo 1991, Goh 1991, Harrison 1993, Richmond 1993, Peters et al. 1997, Palaki 1998, Gilmour 1999, Reichelt-Brushett and Harrison 1999, Negri and Heyward 2000, 2001). Larvae of many marine invertebrates including corals actively select the substrate upon which they settle (Crisp 1974, Keough and Downes 1982, Morse 1990, Pawlik 1992, Morse et al. 1996,

Raimondi and Morse 2000). Appropriate cues for coral settlement include physical stimuli and, in many cases, specific biochemical inducer molecules (Morse et al. 1996, Heyward and Negri 1999, Raimondi and Morse 2000). Factors such as high sediment levels have been shown to inhibit coral larval settlement and persistence (Hodgson 1990, Babcock and Davies 1991, Hunte and Wittenberg 1992, Te 1992, Gilmour 1999). Herbicides, pesticides, heavy metals, oils and dispersants, human drug by-products, and other derived chemical compounds may act as waterborne toxicants that have inhibitory effects on coral recruitment as a result of reactions with larvae, settlement inducer molecules, and/or inducer-producing communities (Richmond 1993, 1997, Peters et al. 1997, Negri and Heyward 2000, 2001, Reichelt-Brushett and Harrison 2000).

Little is known about developmental stimuli or periods of gametogenesis for corals in Hawai'i. Studies of corals in other regions demonstrate that gametogenesis may begin from 2.5 to over 15 months before gamete or planula release (Wallace 1985, Babcock et al. 1986, Szmant 1986, Harrison and Wallace 1990). In Hawai'i, the discharge of coral reproductive products tends to take place over the course of 1 to 2 hours at a predictable time and appears in some cases to correspond to a particular lunar cycle (Table 1). Release recurs in many species over a number of consecutive days, with populations spawning over two to four consecutive months or planulating throughout the year (Table 1). Gamete viability limits the period of fertilization to within hours of spawning (Heyward and Babcock 1986, Hodgson 1988, Hunter 1988a, Oliver and Babcock 1992, Kenyon 1994, Mate et al. 1998). Embryonic development may proceed on the order of days (Babcock and Heyward 1986, Hunter 1988a, Harrison and Wallace 1990, Richmond 1997, Mate et al. 1998; S.P.K., unpubl. data). Coral larvae recruit year-round, but the vast majority of settlement takes place during summer and fall subsequent to spawning of the most abundant species (Fitzhardinge 1993; S.P.K., unpubl. data; E. K. Brown, unpubl. data). Long periods of growth on the order of months to

years may be required before metamorphosed polyps recruit to the visible (sensu Wallace 1983) coral population (S.P.K., unpubl. data; E. K. Brown, unpubl. data).

Hawaiian species for which observations on reproductive mode and timing remain to be made tend to be less abundant, have low population densities, and/or are less accessible in their Hawaiian distributions. Few reports on the reproductive habits of these species in other locations were found (*Gardineroseris planulata* [Glynn et al. 1996], *Pocillopora eydouxi* [Kinzie 1993], *Porites rus* [Richmond and Hunter 1990]). Intraspecific variation in spawning times, sex, and/or modes across geographic distributions for many scleractinian species (see Harrison and Wallace 1990, Richmond and Hunter 1990, Ward 1992, Richmond 1997, Glynn et al. 2000) suggests that inferences on the reproductive timing and characteristics of species yet to be investigated in Hawaiian waters need be made with caution or not at all.

Hawaiian corals do not appear to be unique with regard to reproductive mode and timing. Discrete species gamete release over the course of several days and months has been noted in various geographic regions (Richmond and Hunter 1990, Hayashibara et al. 1993, Richmond 1997) and may increase reproductive success by allowing species to take advantage of environmental variability over time (Harrison and Wallace 1990, Richmond and Hunter 1990). Extended planulae release and spawning across spring and summer months is common to corals in other areas (Richmond and Hunter 1990, Richmond 1997). Mass overlap of species spawning as has been found in areas such as the Great Barrier Reef and Japan (Harrison and Wallace 1990, Richmond and Hunter 1990, Hayashibara et al. 1993) is not apparent in Hawaiian waters. Causal factors of mass spawning events have yet to be resolved. The probability of mass species spawning in Hawai'i is presumably lower because of the relatively depauperate scleractinian species richness of the region.

Sound natural resource management and conservation must be based on a detailed understanding of reef processes if we are to

successfully develop coastal areas in a manner that minimizes impacts to coral reef ecosystems. Our current ability to assess human impacts on coral reproductive dynamics is limited by a number of factors, including natural variation in reproduction, complex and/or synergistic physiological responses of corals to stresses, the lack of a catalog of known impacts and their sources, and incomplete knowledge of coral regional metapopulation boundaries. A few general precautionary guidelines, however, can be made. In particular, special attention should be given to minimizing benthic impacts, including chronic reductions in light, year-round, encompassing all periods of gamete development, recruitment, and growth of all Hawaiian coral species. Dredging or other damaging activities, including mitigation efforts such as the transplantation of corals, should be scheduled to follow the reproductive season of species that will be physically impacted. Changes in water column parameters, such as from fine-grained sedimentation, oil, petrol, and toxic chemical releases, are likely to have the greatest impact when they occur during April through November, the period of synchronous gamete release, fertilization, embryonic development, and dispersal of the dominant Hawaiian corals (Figure 1). Investigations of the effects of steroids, hormones, and other chemical pollutants are needed, as is information on gametogenesis and recruitment processes for all, and reproductive timing, mode, and plasticity for many Hawaiian coral species.

Successful corals tend to be long-lived and experience multiple reproductive events, thus short-term, infrequent, limited, or controlled disturbances might have a negligible long-term impact on reproduction and population dynamics. Further studies of the reproductive biology of Hawaiian corals will elucidate the magnitude of these types of impacts on the long-term dynamics of coral populations. It is important to recognize, however, that the focus of attention should not be restricted to corals, but expanded to cover the range of contributors to reef ecosystem functions, including other invertebrates, vertebrates, plants, algae, and protists.

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